

Spinnerets Silk Spigots Morphology of Araneidae, Tetragnathidae, Theridiidae and Linyphiidae (Araneae: Araneoidea)

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(クモ目: コガネグモ上科) の糸疣と出糸管の形態

Abstract The morphology of spinnerets silk spigots in araneoid species was studied mainly with SEM. Adult females of Araneoidea had two pairs of ampullate spigots and three pairs of cylindrical ones, and most of them had a pair of flagelliform spigots and two pairs of aggregate ones on their spinnerets. These results appeared to be the evidence for the monophyly of Araneoidea. Families of Araneoidea could be distinguished from each other by the differences in the silk spigots morphology. For example, Theridiidae had huge aggregate spigots. Silk spigots morphology was also shown to be useful for re-examining the taxonomic position of species. For example, *Achaearanea* and *Theridion* included the species both with a pair of aggregate spigots and with two pairs of the spigots. It was also shown that the number of aciniform spigots and the size of aggregate spigots were related to the difference in predatory behavior of spiders.

There are many studies on the morphology of silk glands and silk spigots in spiders (e.g., Apstein 1889, Hopfmann 1935, Kovoov 1972, 1987, Peters 1955, Saito 1937, Sekiguchi 1952, 1955a, 1955b), however, such morphological data have been rarely used by taxonomists. This is probably because morphological details can be observed clearly only by using scanning electron microscope and such work is extremely time-consuming. Coddington (1989) developed an elegant system to study spinneret silk spigots in the use of SEM, including the selection of materials, the squeeze of spinnerets by a forceps, ultrasonic cleaning, cleaning spigots with trypsin, by using a steel rivet as a stub of SEM. Nevertheless, the study using SEM, especially the preparation of materials, is probably still time consuming for most researchers.

Recently, a new type of SEM by which raw materials can be observed has been developed, though the resolution is far lower than the materials observed under vacuum and the clear picture can be obtained only at the magnification lower than 500X. This method can be performed without dehydration through an alcohol series up to anhydrous ethanol, vacuum suction drying. In this study, I report many spinnerets of spiders of Araneoidea using both new and old types of SEM. I suggest that the morphology of spinneret silk spigots is useful to characterize families, genera, and species of Araneoidea. Furthermore, I also suggest that silk spigots morphology is useful to

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explain the difference in the hunting behavior of araneoid spiders.

Materials and Methods

1) Species examined

I observed the spinnerets of adult female spiders belonging Tetragnathidae, Araneidae, Theridiidae and Linyphidae (Table 1), using both an optical microscope (Olympus CHS) and a scanning electron microscope (Hitachi S-2460N). In the latter case, spinnerets were observed with SEM mode or N-SEM mode of the electron microscope. Photos were taken by the microscope. The number of spigots of each silk glands were counted mainly by the photos. If the number could not be counted by the photos, I counted it by the observation on another sample of the same species under the SEM or the optical microscope.

2) The preparations for SEM

The preparations for the observations with SEM mode were made by the followings. 1) For living spiders, they were killed by sudden immersion in boiling water in order that the spinnerets were spread widely. In order to stiffen the materials, the spiders were preserved in 70% alcohol for two months. If the spinnerets were not spread, I spread them using a cross-action forceps and preserved them with the forceps in 70% alcohol. For the specimens preserved in 75% alcohol for several years, I selected the spiders whose spinnerets were spread. If the spinnerets were not spread but the abdomen was flexible, I spread the spinnerets by a cross-action forceps and preserved them for several days in order to fix the condition. 2) I served the tip of the abdomen with a razor for large spiders, and preserved in 80% alcohol for an hour (For small spiders, the whole bodies were preserved). 3) The materials were run through an alcohol series up to anhydrous ethanol, and then preserved in iso-amyl acetate. 4) The debris of materials was removed in an ultrasonic cleaner for a few minutes, and then dried by vacuum suction. 5) The materials were coated with silver and were observed with SEM.

3) The preparations for N-SEM

I omitted the processes of dehydration, ultrasonic cleaning, vacuum suction drying, and coating silver on materials, when observed with N-SEM mode. The materials were dried naturally for more than twenty minutes before observation.

Results

1) Number of silk spigots on spinnerets

Figs. 1-14 show the micrographs of spinnerets of araneoid spiders. Table 1 shows the number of spigots on each spinnerets.

Ampullate spigots

There were two ampullate spigots. A major ampullate spigot was on the inner mesal border of the ALS (anterior lateral spinneret) and a minor ampullate spigot on the posterior margin of PMS (posterior median spinneret), respectively (Table 1, Figs. 1-14).

Cylindrical spigots

Spiders had three cylindrical spigots, one on the PMS and two on the PLS (posterior lateral spinneret), respectively (Table 1, Figs. 1-3, 5, 10, 11, 13). The former was on the anterior margin of PMS, and the latter usually on the basal margin of PLS.

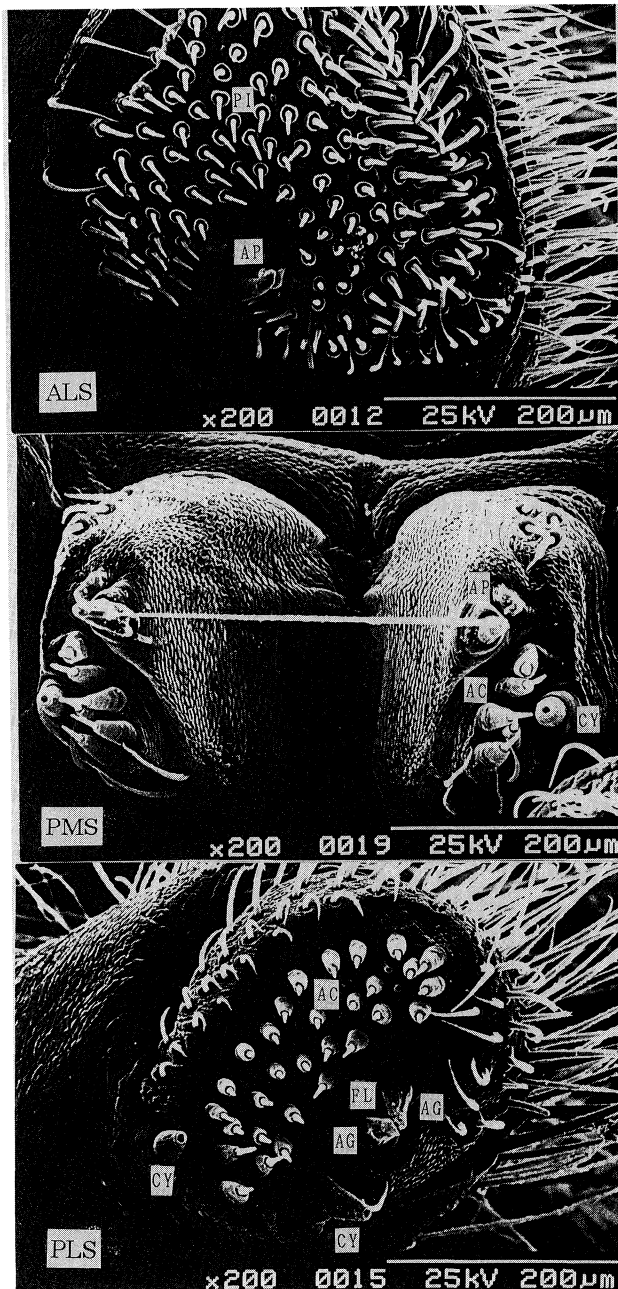


Fig. 1. Spinnerets and spigots of *Metleucauge kempirensis* (Tetragnathidae). ALS: anterior lateral spinneret, PMS: posterior median spinneret, PLS: posterior lateral spinneret, AP: ampullate spigot, PI: piriform spigot, AC: aciniform spigot, CY: cylindrical spigot, AG: aggregate spigot, FL: flagelliform spigot.

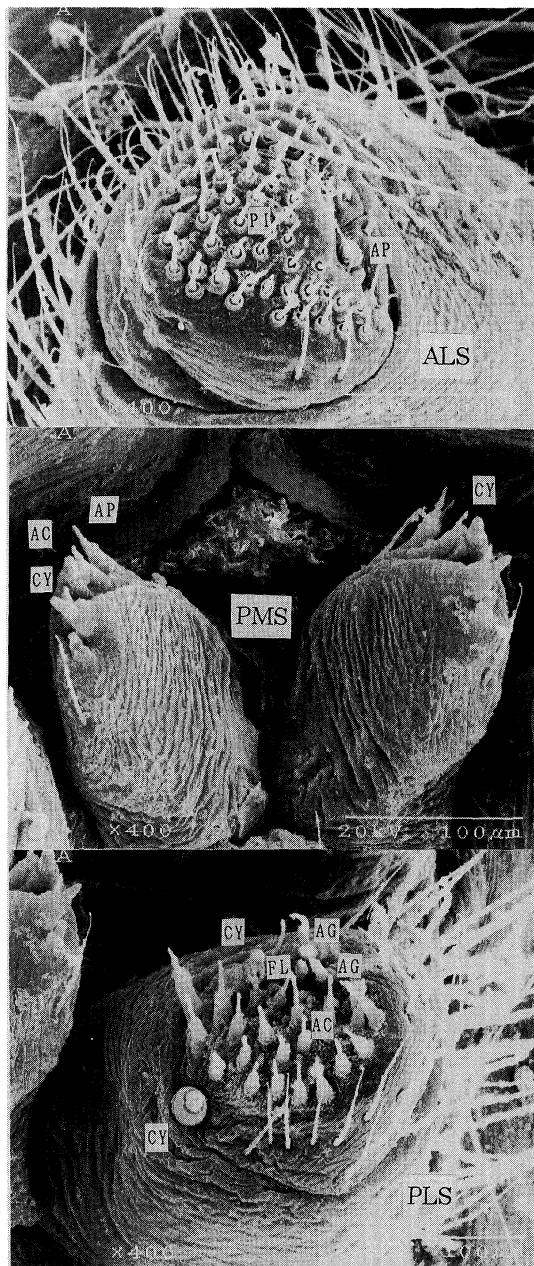


Fig. 2. Spinnerets and spigots of *Meta nigradorsalis*. Abbreviations as in Fig. 1.

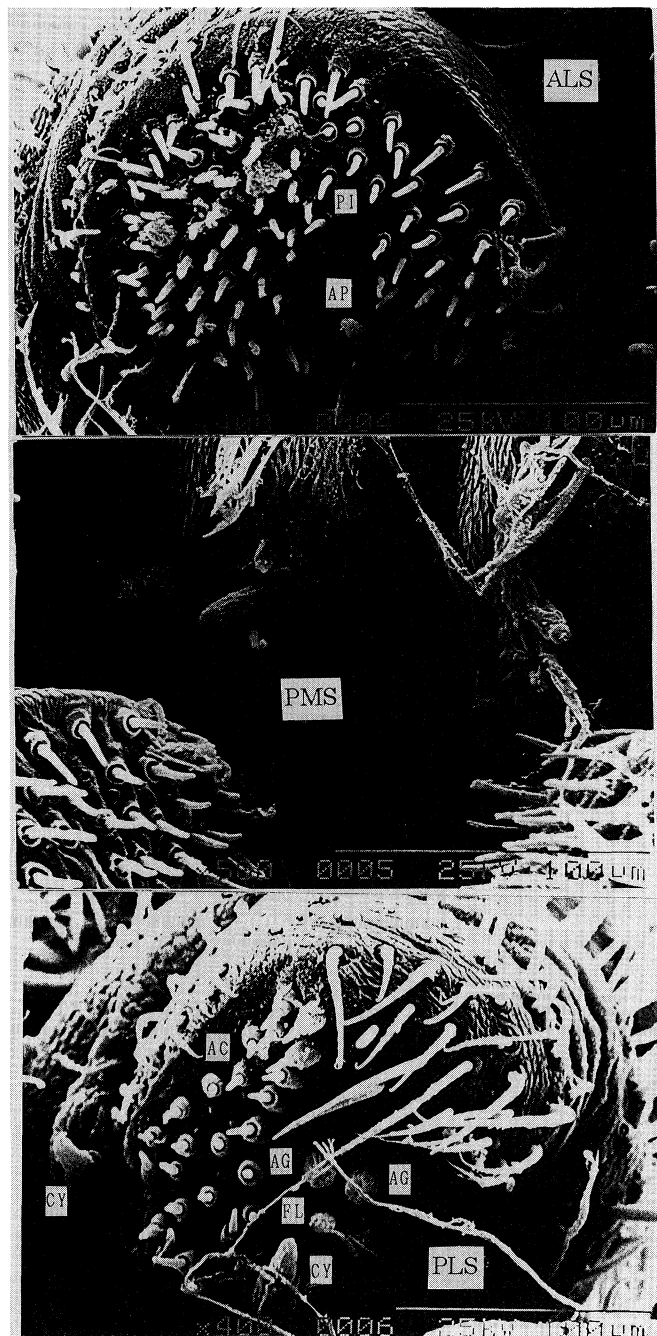


Fig. 3. Spinnerets and spigots of *Tetragnatha praedonia*. Abbreviations as in Fig. 1.

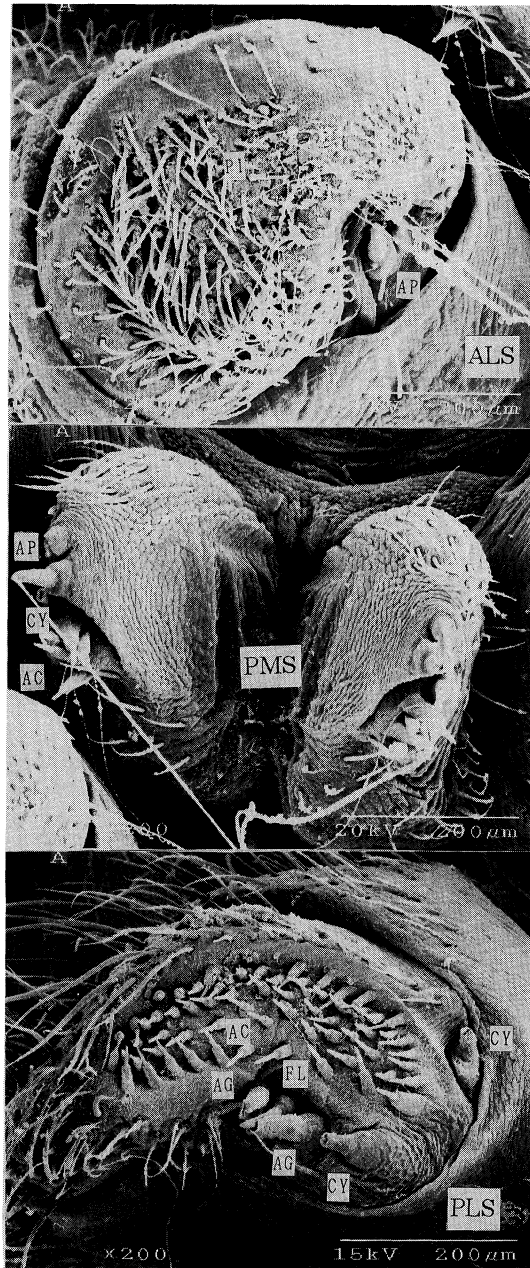


Fig. 4. Spinnerets and spigots of *Nephila clavata*. Abbreviations as in Fig. 1.

Flagelliform spigot

Spiders had usually only one flagelliform spigot on the inner mesal border of the PLS (Figs. 1–6, 8–11, 13, 14), however, *Argyrodes fissifrons*, *A. flavescens* and *A. cylindrogaster* did not have the flagelliform spigot (Fig. 12). *A. saganus* had a flagelliform spigot at the site where there was a smaller aggregate spigot in the other species of *Argyrodes* (Fig. 13).

Aggregate spigots

Spiders had two aggregate spigots on the PLS (Table 1, Figs. 1–6, 9–12) except *Achaearanea japonica*, *Theridion sterninotatum*, and *Argyrodes saganus*. The three species had only one large aggregate spigot (Fig. 8, 13).

Piriform spigots

Spiders had many piriform spigots on the ALS, though there were large differences in the number among species or families (Table 1). Araneid spiders had a large number of piriform spigots (ca. 65 in *Neoscona mellottei* to ca.200 in *Araneus ventricosus*, *Argiope bruennichii* and *Argiope amoena*). Six of eight species of Araneidae had more than 100 piriform spigots. Tetragnathid spiders had ca. 55 (*Meta nigridorsalis*) to ca. 150 piriform spigots (*Metteuauge kompirensis*), and seven of nine species had less than 100 spigots. Theridiid spiders had ca. 20 (*Argyrodes fissifrons*) to ca. 90 (*Achaearanea*

Table 1. Number of spigots on each spinneret. AL: anterior lateral spinneret, PM: posterior median spinneret, PL: posterior lateral spinneret. Numerals in parentheses show the figure number of their micrographs.

	piriform AL	ampullate AL PM	aciniform PM PL	cylindrical PM PL	flagelliform PL	aggregate PL
Tetragnathidae						
<i>Metteuauge yunohamensis</i>	ca. 80	1 1	5	24	1 2	1 2
<i>Metteuauge kompirensis</i> (1)	ca. 150	1 1	5	30	1 2	1 2
<i>Metteuauge yaginumai</i>	ca. 80	1 1	4	19	1 2	1 2
<i>Metteuauge chikunii</i>	60–80	1 1	4	18	1 2	1 2
<i>Meta nigridorsalis</i> (2)	ca. 55	1 1	4	20	1 2	1 2
<i>Laucauge magnifica</i>	ca. 60	1 1	3	26	1 2	1 2
<i>Tetragnatha praedonia</i> (3)	ca. 90	1 1	2	24	1 2	1 2
<i>Tetragnatha maxillosa</i>	ca. 90	1 1	2	17	1 2	1 2
<i>Nephila clavata</i> (4)	ca. 120	1 1	5	ca. 60	1 2	1 2
Araneidae						
<i>Larinioides cornutus</i> (5)	ca. 110	1 1	ca. 25	ca. 60	1 2	1 2
<i>Araneus ventricosus</i>	ca. 200	1 1	ca. 110	ca. 250	1 2	1 2
<i>Araneus ishisawai</i> (6)	ca. 180	1 1	ca. 170	ca. 250	1 2	1 2
<i>Yaginumia sia</i>	ca. 110	1 1	ca. 22	ca. 50	1 2	1 2
<i>Neoscona mellottei</i>	ca. 65	1 1	ca. 60	ca. 75	1 2	1 2
<i>Argiope minuta</i>	ca. 80	1 1	ca. 100	ca. 150	1 2	1 2
<i>Argiope bruennichii</i> (7)	ca. 200	1 1	ca. 100	ca. 200	1 2	1 2
<i>Argiope amoena</i>	ca. 200	1 1	ca. 80	ca. 200	1 2	1 2
Theridiidae						
<i>Achaearanea japonica</i> (8)	53	1 1	2	8	1 2	1 1
<i>Achaearanea tepidarium</i> (9)	ca. 90	1 1	2	10	1 2	1 2
<i>Achaearanea kompirensis</i>	ca. 35	1 1	2	6	1 2	1 2
<i>Theridion chikunii</i> (10)	ca. 30	1 1	2	4	1 2	1 2
<i>Latrodectus hasselti</i> (11)	ca. 55	1 1	3	7	1 2	1 2
<i>Argyrodes fissifrons</i> (12)	ca. 20	1 1	3	8	1 2	1 2
<i>Argyrodes saganus</i> (13)	ca. 25	1 1	3	9	1 2	1 1
Linyphiidae						
<i>Linyphia longipedella</i> (14)	ca. 45	1 1	3	6	1 2	1 2
<i>Linyphia nigripictoris</i>	ca. 20	1 1	3	7	1 2	1 2



Fig. 5. Spinnerets and spigots of *Larinioides cornutus*. Abbreviations as in Fig. 1.

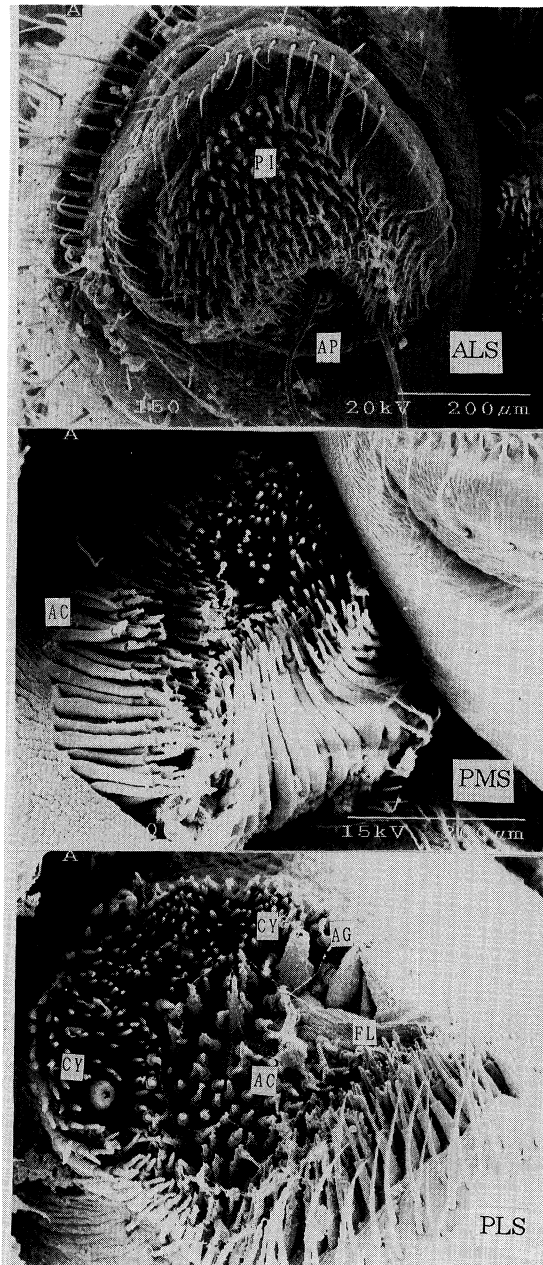


Fig. 6. Spinnerets and spigots of *Araneus ishisawai*. Abbreviations as in Fig. 1.



Fig. 7. Spinnerets and spigots of *Argiope bruennichii*. Abbreviations as in Fig. 1.

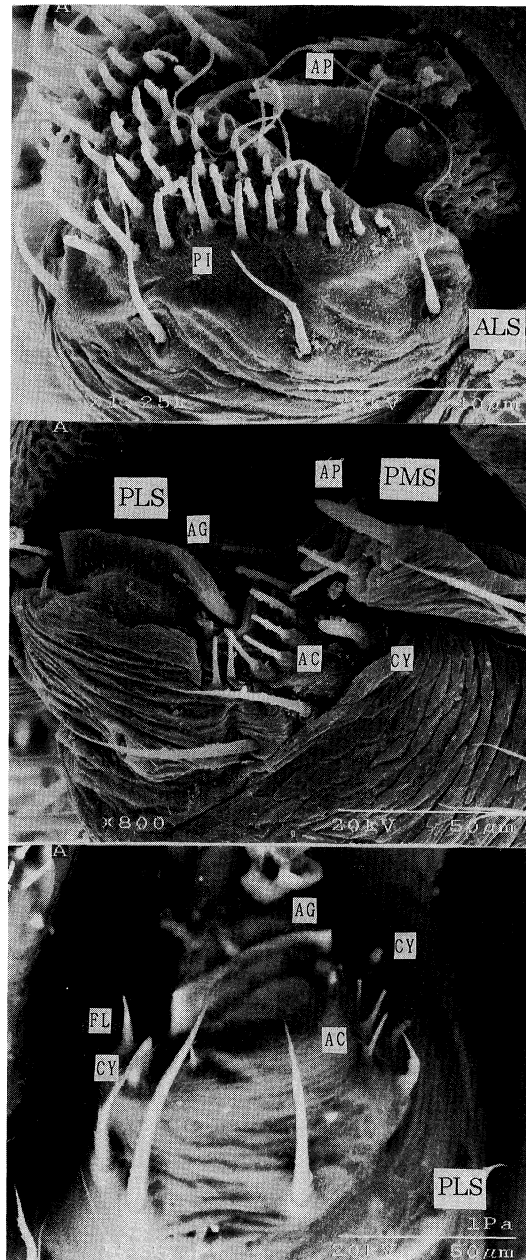


Fig. 8. Spinnerets and spigots of *Achaearanea japonica*. Abbreviations as in Fig. 1.

tepidariorum), and six of seven species had less than 60 spigots. Two linyphiid species had ca. 20 to ca. 45 spigots.

Aciniform spigots

Aciniform spigots were found both on the PMS and the PLS. On the PMS, araneid spiders had ca. 25 (*Larinioides cornutus* and *Yaginumia sia*) to ca. 170 (*Araneus ishisawai*) aciniform spigots. *Araneus* (two species) and *Argiope* (three species) had a large number of aciniform spigots (Table 1, Figs. 5–7). On the contrary, spiders of other families had a very small number (less than 10) of aciniform spigots on

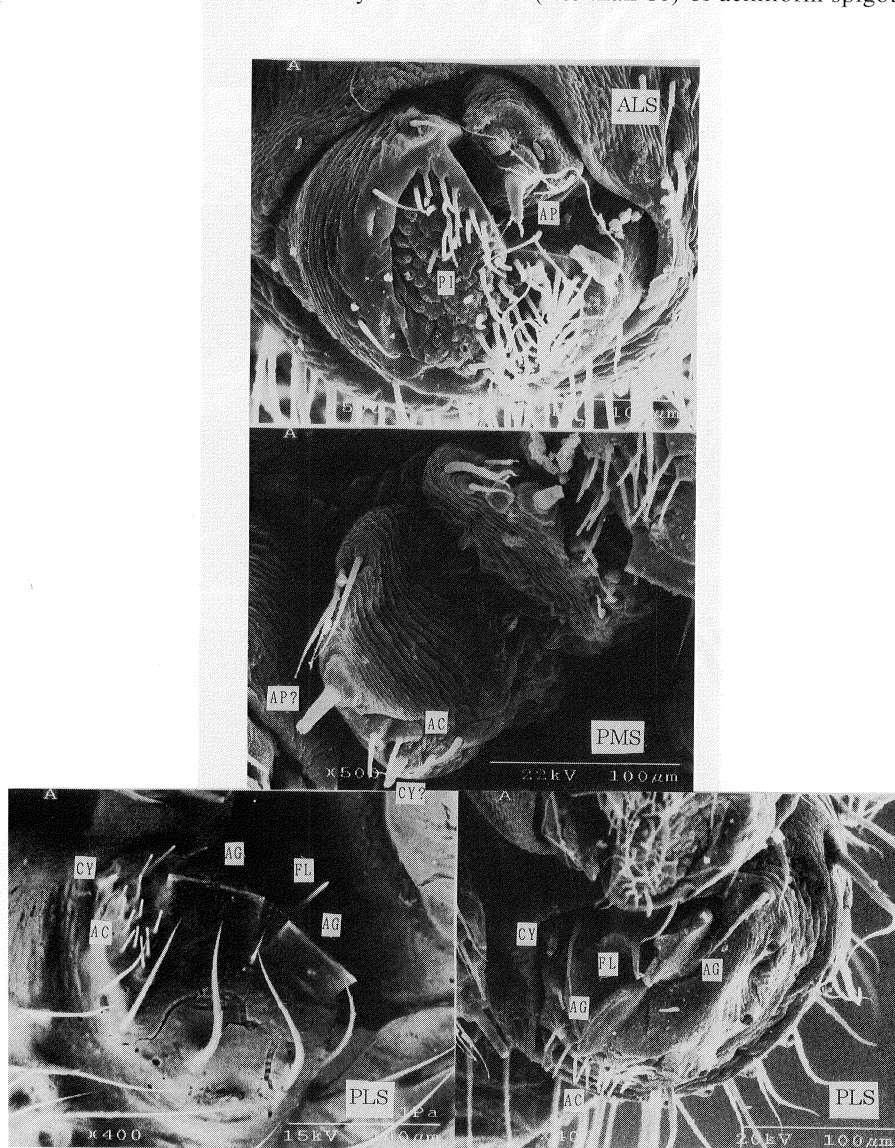


Fig. 9. Spinnerets and spigots of *Achaeranea tepidariorum*. Abbreviations as in Fig. 1.

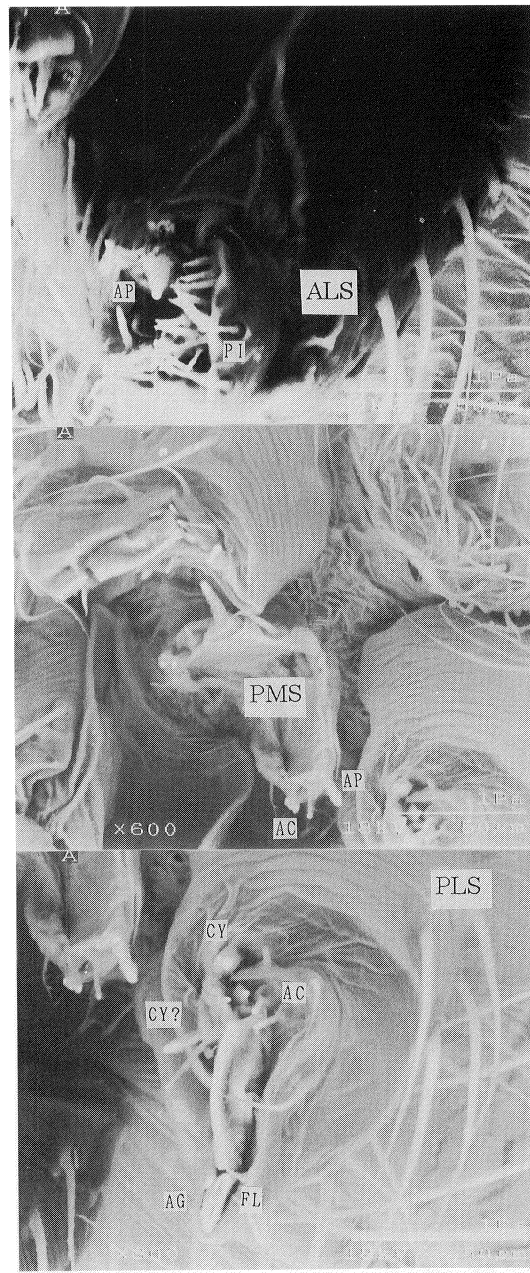


Fig. 10. Spinnerets and spigots of *Theridion chikunii*. Abbreviations as in Fig. 1.

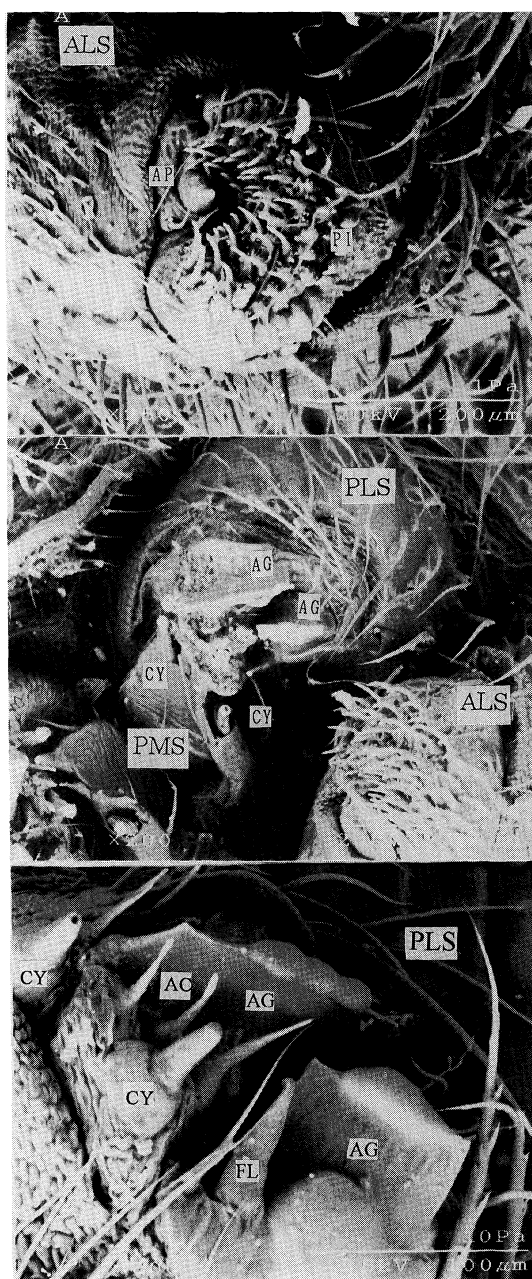


Fig. 11. Spinnerets and spigots of *Latrodectus hasselti*. Abbreviations as in Fig. 1.

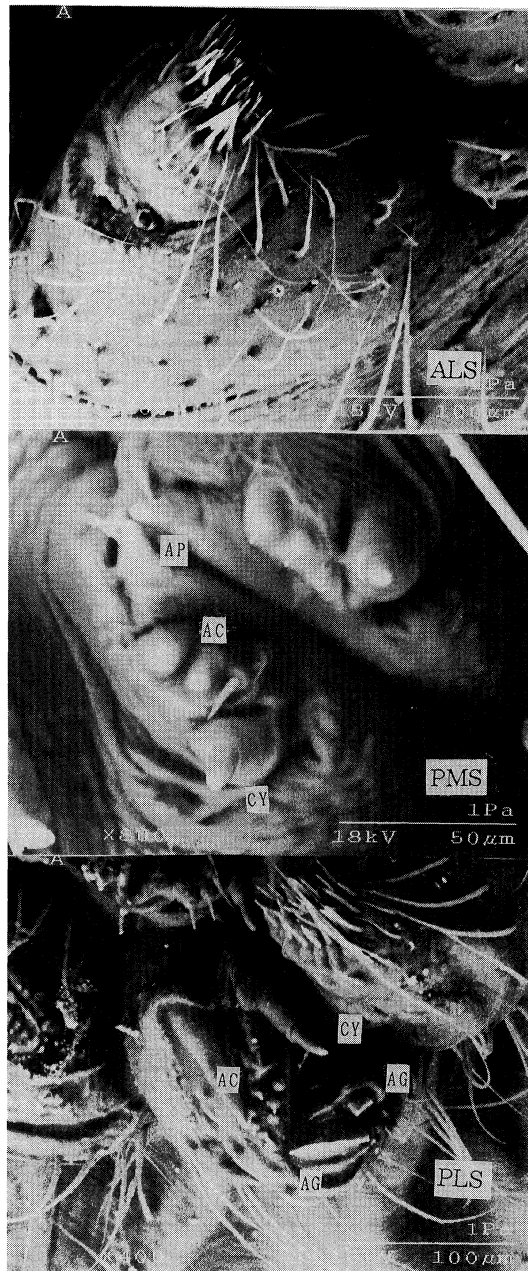


Fig. 12. Spinnerets and spigots of *Argyrodes fissifrons*. Abbreviations as in Fig. 1.

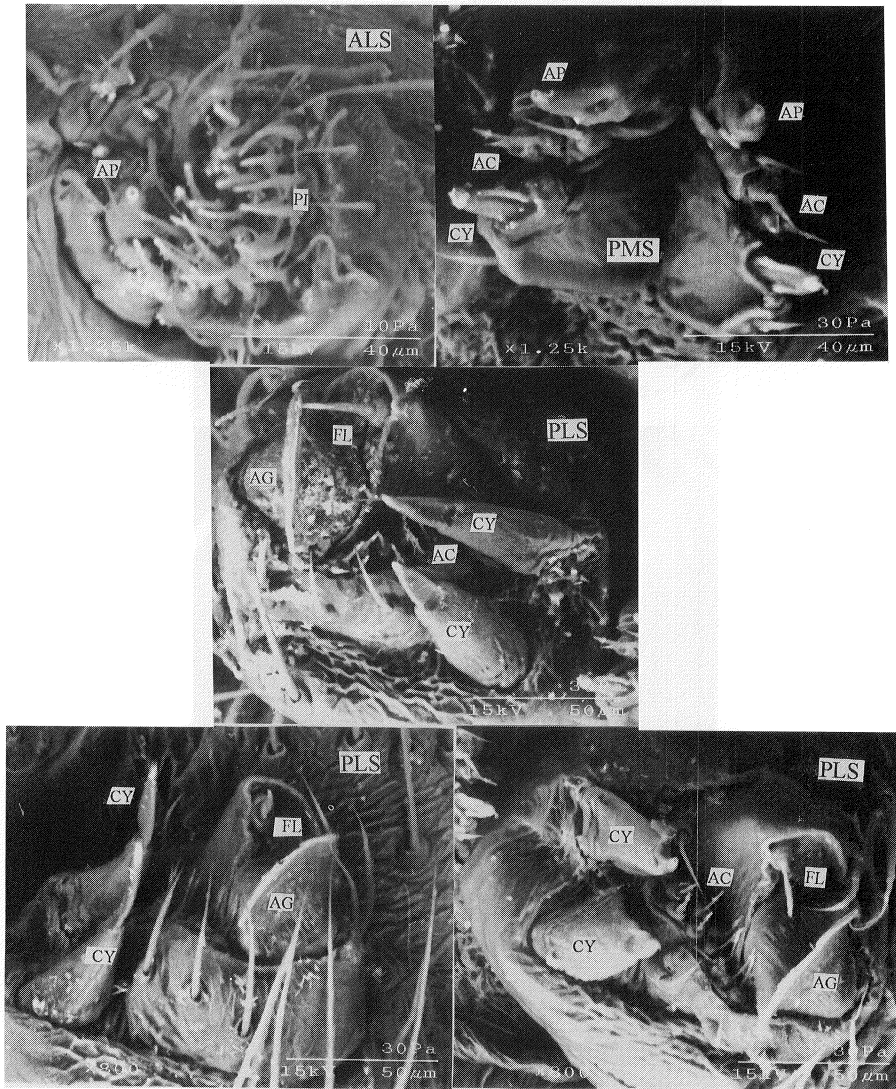


Fig. 13. Spinnerets and spigots of *Argyrodes saganus*. Abbreviations as in Fig. 1.

the PMS (Table 1, Figs. 1–4, 6–14).

Spiders had more number of aciniform spigots on the PLS than on the PMS. Araneid spiders had a larger number of aciniform spigots on the PLS than spiders of other families (especially Theridiidae and Linyphidae), as also found on the PMS (Table 1).

There were differences in the number of aciniform spigots on the PLS of *Leucauge magnifica* from 25 to 28 among eight individuals. Half of them had twenty-six

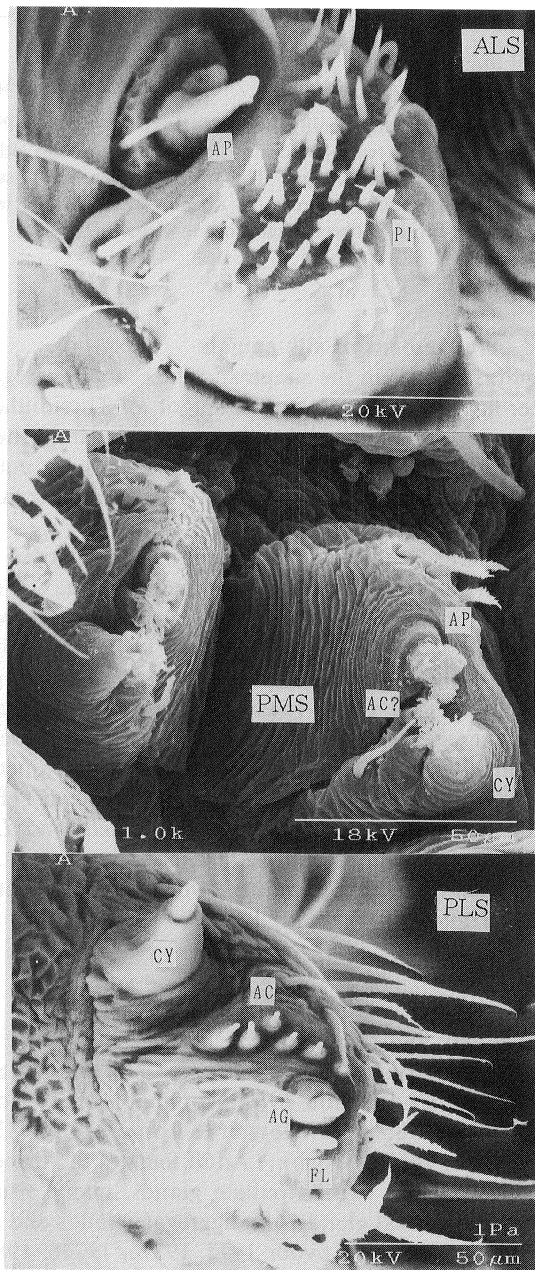


Fig. 14. Spinnerets and spigots of *Linyphia longipedella*. Abbreviations as in Fig. 1.

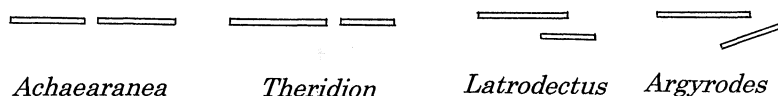


Fig. 15. The arrangement of the openings of aggregate spigots on each PLS in theridiid genera. *Achaearanea* had two openings of similar size, however, other genera had one small and one large openings. The openings were on a straight line in *Achaearanea* and *Theridion*, whereas the openings ran parallel in *Latrodectus*. The direction of openings differed each other in *Argyrodes*.

aciniform spigots.

2) Shape, size and arrangement of silk spigots

There were large differences in the shape and the size of aggregate spigots between Theridiidae and other families. The aggregate spigots of Theridiidae were much larger than those of other families, and appeared to be rectangular from the size of view (Figs. 8, 9, 11–13). The opening from which adhesive substance is put out looked like a long slit (Fig. 9, 10). On the other hand, the aggregate spigots of other families were smaller, and looked like cones (Figs. 1–5, 14).

There were also differences in the arrangement of silk spigots. In Tetragnathidae, the flagelliform spigot of *Metleucauge*, *Leucauge* and *Nephila*, was sandwiched by two aggregate spigots (Figs. 1, 4, 9), however, a flagelliform spigot and two aggregate spigots of *Meta* and *Tetragnatha* formed a triangle on the PLS (Figs. 2, 3).

Furthermore, there were also differences in the size and the arrangement of aggregate spigots among theridiid genera (Fig. 15). *Achaearanea* (*A. tepidariorum* and *A. komprensensis*) had two aggregate spigots of similar size (Fig. 9), whereas other genera had one large and one small spigots (Figs. 10–12, 15). The slit-like openings of two spigots were on a straight line in *Achaearanea* and *Theridion* (*T. chikunii*) (Figs. 9, 10), whereas they were apart from each other in *Latrodectus* (*L. hasselti* and *L. geometricus*) and *Argyrodes* (*A. fissifrons*, *A. flavescens* and *A. cylindrogaster*) (Figs. 11, 12, 15). Two openings ran parallel each other in *Latrodectus* whereas the direction of two openings differed each other in *Argyrodes* (Figs. 11, 12).

Discussion

1) Silk spigot morphology and taxonomy

There are many studies on the morphology of silk glands and silk spigots of Araneoidea (Apstein 1889, Coddington 1989, Hopfmann 1935, Hormiga *et al.* 1995, Kooor 1972, 1977a, 1977b, 1986, 1987, Kooor & Lopez 1982, 1983, 1988, Peters 1955, Saito 1937, Sekiguchi 1952, 1955a, 1955b). Adult females of Araneoidea usually have six types of silk glands, that is, two ampullate glands, many piriform glands, many aciniform glands, three cylindrical glands, two aggregate glands and a flagelliform gland (Sekiguchi 1955a, Yoshikura 1987, Kooor 1972, 1977a, 1977b, 1986, 1987, Kooor & Lopez 1982, 1983, 1988, Coddington 1989). These findings are consistent with the results in the present study.

However, there are some exceptions (Kooor & Lopez 1982, 1983). Three species of *Cyrtophora* do not have aggregate and flagelliform glands (Kooor & Lopez 1982), and twelve species of *Argyrodes* do not have flagelliform spigots (Kooor & Lopez

1983). *Argyrodes cylindrogaster* and *A. flavescens* also did not have flagelliform spigots, as shown in this study.

Coddington (1989) first used silk spigots morphology in spider phylogeny. He took the scanning electron micrographs of Deinopidae, Uloboridae, Araneidae, Tetragnathidae, Theridiidae, Nesticidae and Linyphidae, and argued the monophyly of orb-weaving spiders, Cyrtophorinae, and the group Theridiidae-Nesticidae. Several morphological and taxonomical studies on spinnerets silk morphology with scanning electron microscope have been published (Coddington 1990, Coddington & Levi 1991, Hormiga *et al.* 1995, Scharff & Coddington 1997, Yoshida 1996).

The comparison of silk spigots morphology is useful to analyze the relationships among various levels of taxa. For example, araneid species had more aciniform spigots on the PMS than tetragnathid species (Table 1).

Furthermore, the relative size and the arrangement of aggregate spigots were good characters to distinguish theridiid genera (Fig. 15). It was consistent with the micrographs taken by other researchers (Coddington 1989, Kovoov & Lopez 1983). The direction of two openings of aggregate spigots differed each other in *Argyrodes argentatus* (Kovoov & Lopez 1983), whereas two openings ran parallel each other in *Latrodectus variolus* (Coddington 1989).

The arrangement of aggregate-flagelliform triad is also a useful character to distinguish the genera of Metinae. Hormiga *et al.* (1995) found that there were two types of arrangements among aggregate-flagelliform triad in Tetragnathidae. In one type, aggregate spigots are apart from a flagelliform spigot, whereas in another type, the distal ends of aggregate spigots embrace the distal end of the flagelliform spigot. This difference was also found in this study. For example, though *Meta* and *Metleucauge* are the related genera, *Meta* was the former type, whereas *Metleucauge* was the latter type (Figs. 1, 2). Levi (1980) divided "*Meta*" into three genera, *Meta*, *Metellina* and *Metleucauge*, judging from several morphological differences. His conclusion is therefore supported by the silk spigots arrangement as well. There was also an example with differences in the shape of piriform spigots and the number of aciniform spigots among related genera. *Larinioides* is a genus which was divided from *Araneus* (Grasshoff 1983). The piriform spigots of *Larinioides* were thicker than those of *Araneus*, and the number of aciniform spigots on the PLS of *Larinioides* was much smaller than that of *Araneus* (Figs. 5, 6; Table 1).

Differences were also found among congeneric species. It is noteworthy that *Achaearanea japonica* and *Theridion sterninotatum* did not have two aggregate spigots but had only one spigot (Fig. 8; Table 1). It is strange that there are species with two aggregate spigots and those with only one spigot in the same genera. The taxonomy of the species of *Achaearanea* and *Theridion* should be re-examined based on this large difference of silk spigot morphology. The aggregate spigot of *A. japonica* seemed to have been formed by the fusion of two aggregate spigots which were found in *A. tepidariorum*, because the size of the spigot of the former was nearly two times larger than that of the latter (Figs. 8, 9), although this point must be ascertained by anatomical studies.

There seemed to be differences in the number of aciniform spigots on the PLS among congeneric species. For example, of four species of *Metleucauge*, *M. kompirensis* had the largest number (30), whereas *M. chikunii* had the smallest number (18) (Table 1). However, intraspecific variation was found in the number of spigots. *Leucauge*

magnifica had 25 to 28 aciniform spigots on the PLS. Furthermore, the numbers of spigots counted in this study were different from those reported by other authors in some species (Saito 1937; Sekiguchi 1955a). For example, the number of aciniform spigots on the PLS of *Tetragnatha praedonia* was 24 in this study (Table 1), whereas that reported by Sekiguchi (1955a) was 16. Therefore, intraspecific variation must be fully investigated in order to decide whether or not the number of silk spigots is an useful character.

2) Predatory behavior and silk spigots morphology

The morphology of spinnerets silk spigots is also useful to compare behavior and web structure of spiders. For example, Kovoov & Lopez (1982) stated that the lack of aggregate-flagelliform triad in *Cyrtophora* might be due to the absence of sticky spirals in the web. Hunting manner seems to be related to the number of aciniform spigots of spiders in Araneidae and Tetragnathidae. Many araneid genera such as *Argiope* and *Araneus* cast swathes of silks to their prey being captured by the webs. This behavior is called as "immobilization wrapping" or "attack wrapping" (Robinson 1969, 1975, Robinson, Mirick & Turner 1969, Robinson & Olazzari 1971). Several tetragnathid genera such as *Meta*, *Tetragnatha* and *Leucauge* attack their prey also by wrapping with silks (Eberhard 1982, Yoshida 1987, 1990, Yoshida & Shinkai 1993), though it takes a long time for these spiders to wrap prey probably because the silks pulled from aciniform spigots are few (Yoshida 1987, 1990). On the other hand, two tetragnathid genera, *Nephila* and *Metleucauge* never attack their prey by wrapping (Robinson 1975, Robinson, Mirick & Turner 1969, Yoshida 1989). Linyphiid spiders also do not attack their prey by wrapping (Bristowe 1958).

Spiders using attack wrapping are expected to have much larger number of aciniform glands than the spiders lacking attack wrapping. The data on aciniform spigots support this expectation roughly as follows: 1) linyphiid spiders which immobilize prey only by biting, had a small number of aciniform spigots, that is, a few small ones on the PMS and several small ones on the PLS, 2) araneid spiders, most of which immobilize prey effectively by wrapping, had a larger number of aciniform spigots than tetragnathid spiders as shown in this study (Table 1) and in Coddington (1989). However, the following data were not consistent with this expectation: *Nephila clavata* had the largest number of aciniform spigots on the PLS among tetragnathid spiders (Table 1), though this species never wrap to immobilize its prey. This means that morphological characters are not always consistent with behavioral characters. The reason of this inconsistency must be made clear in future studies.

Theridiid spiders never wrap prey by swathes of silks emitted from many aciniform glands, but wrap them by adhesive silk (Kaston 1972). The silk is homologous as the sticky spiral of orb webs made by spiders of other araneoid families, and made of the silk emitted from the flagelliform gland and the sticky substance emitted from aggregate glands. The sticky balls of the silk made by theridiids are so large that one can see them with naked eyes. Though the aggregate glands of theridiid spiders are not so large (Hopfmann 1935), the openings of the aggregate spigots were huge (Figs. 8-12). Hence a large mass of sticky substance may be emitted from the aggregate spigots. On the contrary, theridiid spiders had a few small aciniform spigots on the PMS and several small ones on the PLS (Figs. 8-12). They may be unable to wrap prey with swathes of silks, because the number of aciniform spigots is small. Judging from the smallness of aciniform spigots of theridiid spiders, the aciniform glands may not emit silks.

Kovoor & Lopez (1983) found that twelve species of *Argyrodes* did not have their flagelliform gland, and the aggregate glands were more or less reduced. *Argyrodes fissifrons*, *A. flavescens* and *A. cylindrogaster* did not have their flagelliform spigot as well (Fig. 12; Table 1), probably because these *Argyrodes* never wrap prey.

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摘 要

光学顕微鏡と走査型電子顕微鏡によって、コガネグモ上科に属する4科のクモの糸疣と出糸管を観察した。どの科も2対の瓶状腺、3対の管状腺、および通常2対の集合腺と1対の鞭状腺を持っており、コガネグモ上科が単系統群であることを示唆している。また、出糸管の形や数は、科・属・種によって異なり、これらの形質がコガネグモ上科のクモの分類に有用であることが示された。また、ブドウ状腺の数や集合腺のサイズがクモの捕食行動の違いと関連していることが明らかにされた。

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